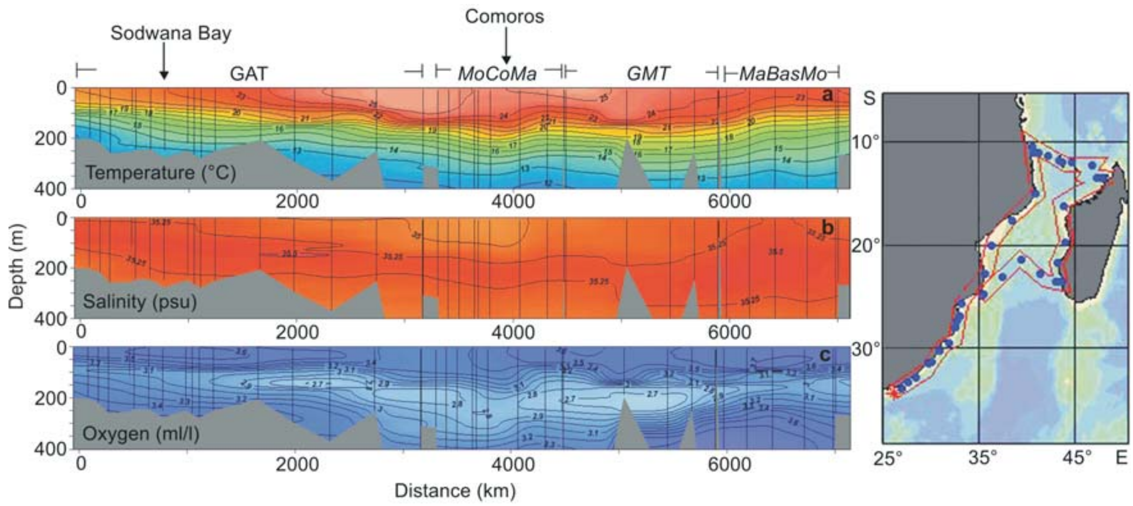

Fig. 7. Composites of CTD data collected along the East African shelf (GAT), across the northern Mozambique Channel (MoCoMa) past the Comoros, the west coast of Madagascar (GMT), and the southern Mozambique Channel (MaBasMo) (see map inset). (**a**) Temperature, (**b**) salinity, and (**c**) dissolved oxygen. Note the temperature range of 15–19°C (green and yellow band) and the SOM become shallower southwards towards Sodwana Bay relative to the tropics.

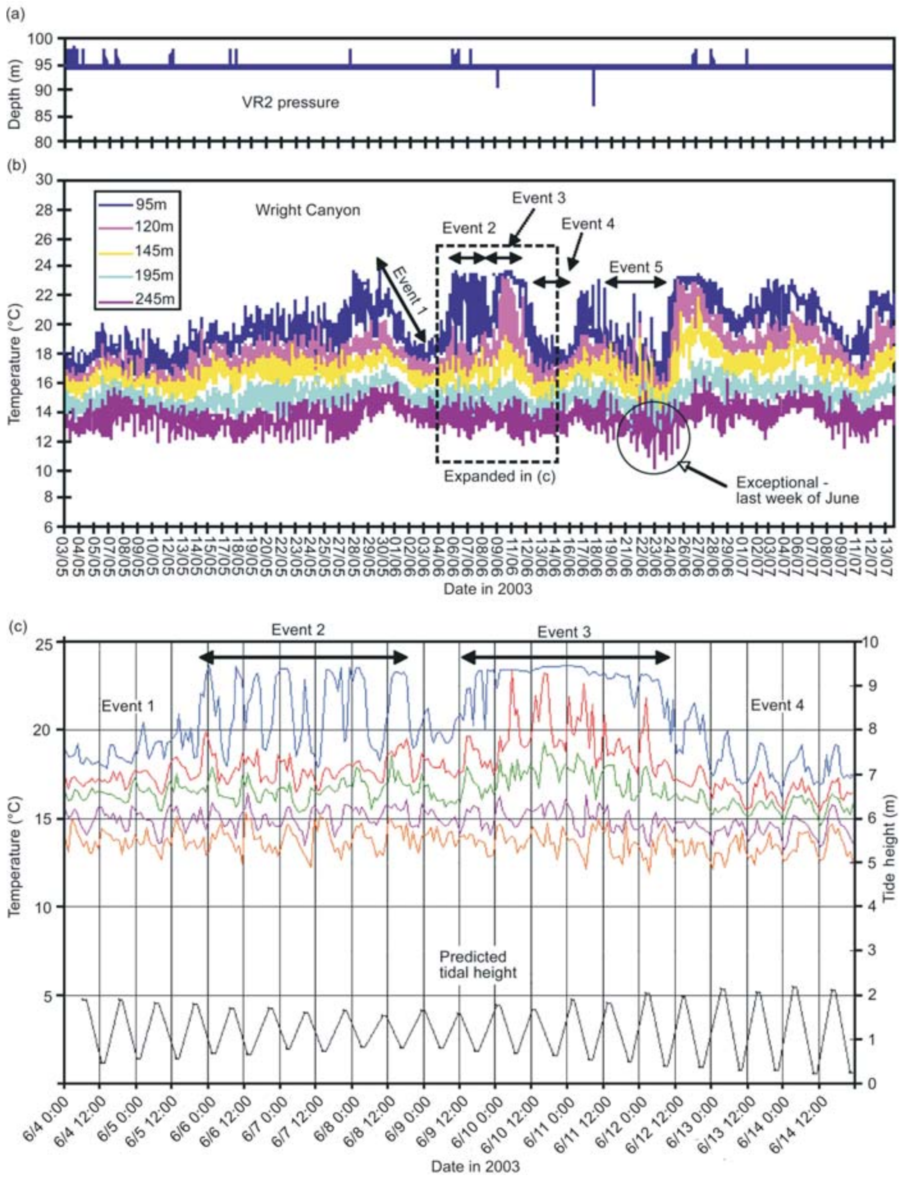

Fig. 8. Data between 3 May 2003 and 13 July 2003 from the thermistor array moored 250 m in a side valley in Wright Canyon. (**a**) Pressure data recorded at the top of the mooring (95 m) show the array to have remained vertical throughout the deployment. (**b**) Hourly temperature data for the depths of 95 m, 120 m, 145 m, 195 m and 245 m (2 m from the bottom). (**c**) Expansion of the data in the dashed box indicated above. Predicted tidal height has also been plotted and shows a good correlation with many of the temperature fluctuations, especially during spring tides.

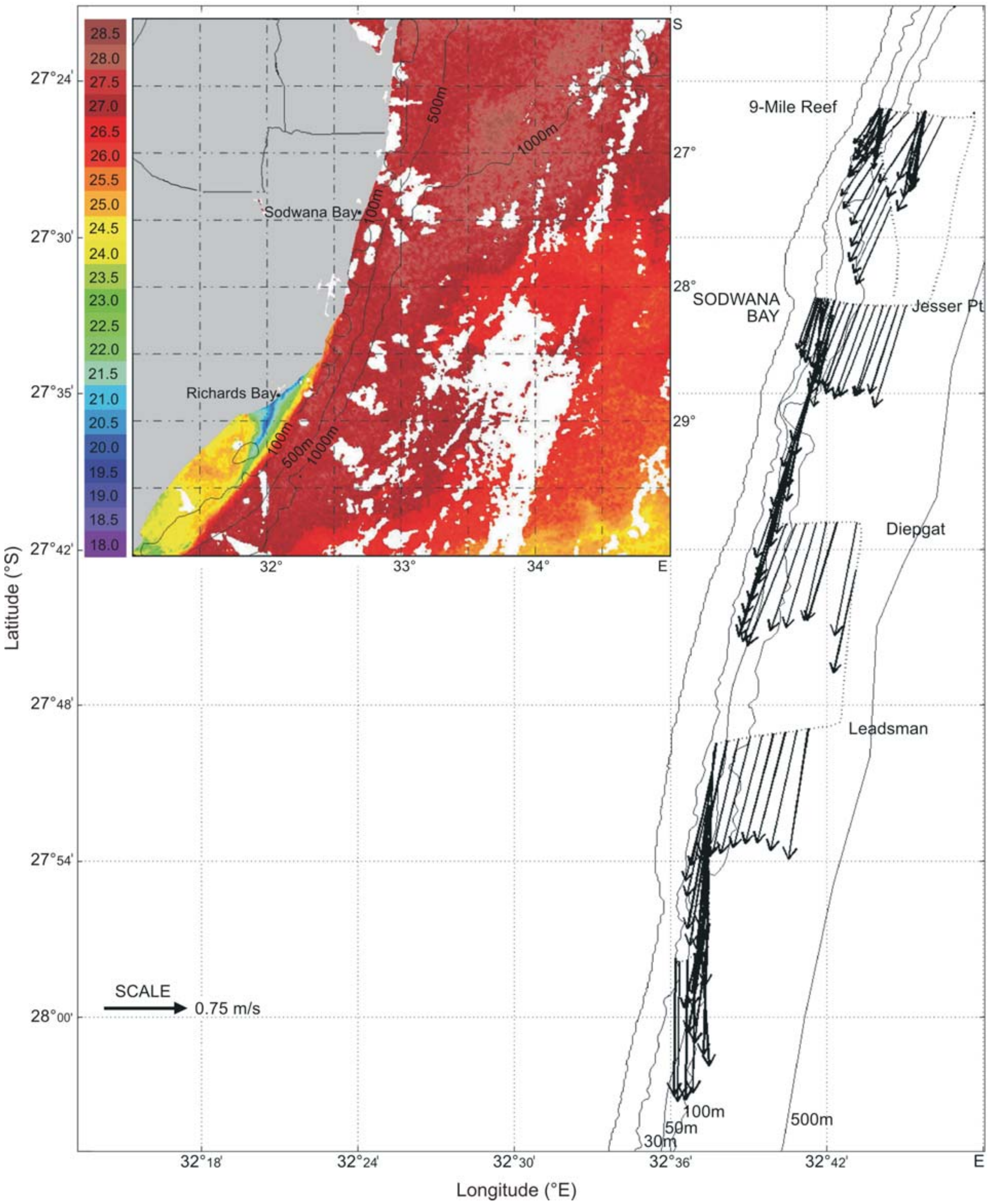

Fig. 9. Velocity data collected on 5 April 2002 using a 150-kHz ship-board ADCP. Stick vectors corresponding to a depth of 12 m indicate a strong southward flow along the shelf edge. SST data in the satellite image (inset) show the Agulhas Current (red) joining the shelf near Sodwana Bay. Scale in °C.

that is, in the coelacanth habitat. It is assumed that because the thermistor array was only 200 m from the side of the canyon, the thermistor data will be representative of temperature against the shelf slope. Below this depth, the range in temperature generally decreased to 2–3°C. The exception was the last week in June, when the range increased to 11–16°C (Fig. 8b).

It is highly probable that the longer-term cooling events, i.e. events 1, 4 and 5, are due to shelf-edge upwelling as a result of the Agulhas Current flowing close to the edge. When this happens, Ekman veering is experienced in the bottom layer, which causes cooler water to move up the slope.[19] Offshore movement of the current a few days later would diminish Ekman veering, resulting in warmer water replacing the cooler water.

The high-frequency fluctuations seen in the temperature records are predominantly linked to tides and the consequent movement of water up and down the continental slope. This is seen in the expanded subset of temperature data in Fig. 8c. The predicted tidal range for the period for the nearest port, Richards Bay, is shown at the bottom of the plot (note that actual tidal height was not available). The maximum tidal range in this area is 1.95 m. The tidal signal is most consistently seen in the deeper temperature data at 195 m and 245 m, in which a good correlation exists (with almost no lag) between a rise in temperature at low tide and a decrease in temperature at high tide. The correlation becomes weak during neap tides when the tidal range is lowest (*c.* 0.8 m). Generally, the tidal signal is also observed in the shallower depth data, but is particularly obvious at 95 m during event 2. Here the large changes in temperature at 95 m are due to the vertical movement of the sharp thermocline at around this depth, i.e. a much greater change in temperature for a given rise and fall of water relative to greater depths where the temperature structure of the water column is less condensed.

In event 3, the situation is almost reversed in that the 95 m data are consistent for 3.5 days at *c.* 23.6°C, while the 120 m data show large temperature fluctuations which strongly correlate with the tidal signal. The only explanation for this is that the sharp thermocline impinging on the shelf slope was deeper on this occasion at around 120 m and that the 95 m UTR was positioned in the warm upper mixed surface layer—a situation similar to that depicted in Fig. 4a, where the thermocline is downward tilting onto the slope.

Thermistor data have shown that temperature in the coelacanth habitat at Sodwana Bay is not as stable as that portrayed by the CTD data and emphasizes the importance of moorings; it is highly variable, ranging between 13 and 24°C with large fluctuations of up to 5°C occurring over only a few hours. However, it may be that coelacanths can avoid this rapid and high variability by moving into deep caves where water exchange will be limited and hence temperatures more stable. This needs to be tested by deploying UTRs outside and inside caves at Sodwana.

The inverse situation, that is, coelacanths in warmer water inside a cave than out, was noted in the Comoros by Fricke *et al.*,[20] with a thermocline appearing within the cave (see their Fig. 10). The fish in the cave were at 22.8°C, when outside it was 18°C. They also suggested that the upper threshold limit for coelacanths is 22–23°C. This suggests that coelacanth distribution might be affected more by the presence of appropriate shelter than temperature.

Oxygen

Figure 2b shows a typical dissolved oxygen (DO) vertical profile found off Sodwana Bay. DO at the surface in all the CTD transects sampled was found to be approximately 3.6 ml l^{-1} with bottom values at a depth of 1000 m of *c.* 3.2 ml l^{-1}. A shallow oxygen minimum (SOM) of *c.* 3.2 ml l^{-1} was observed in all data between the depths of 100 and 250 m. Immediately below this, the DO increased to values similar to the surface, i.e. 3.6 ml l^{-1}, before decreasing to the lower levels at 1000 m. The SOM therefore meets the continental slope at the depths where the Sodwana Bay coelacanths have been found (100–140 m). DO values extracted for 100 m and 140 m in all transects are listed in Table 1 and ranged between 3.0 and 3.2 ml l^{-1}.

The SOM is a characteristic found throughout most of the South-West Indian Ocean. As seen in Fig. 7 it overlaps the 15–19°C layer mentioned above and hence follows a similar trend, being deeper in the equatorial regions and shallower in the south adjacent to the African continent. Near the Comoros these data (collected in August 2003) show SOM values of 2.9 ml l^{-1} in the depth range of 200–325 m in which coelacanths are found. The Sodwana Bay SOM levels reported here are of a similar level to those at the Comoros in Fig. 7. Interestingly, Hissmann *et al.*[4] measured DO values of 3.5 ml l^{-1} at cave entrances in the Comoros, indicating some variability in the coelacanth habitat there.

The significance of varying levels of DO on the physiology of the coelacanth is not yet understood. Work by Hughes and Itazawa[18] suggests that the optimum temperature for the uptake of oxygen in coelacanth haemoglobin is 15°C. This implies that the Sodwana coelacanths should rather be living at greater depths of around 200 m instead of 100–140 m. However, observations from submersible indicated there are fewer caves deeper than 140 m (that is, below the Pleistocene terraces[3]) and so it is possible, given their apparent affinity to caves, that these coelacanths could become stressed when water temperature increases substantially above the optimal oxygen uptake temperature of 15°C.

Currents

An ADCP survey was undertaken along the shelf edge between 9-Mile Reef and Leven Canyon on 5 April 2002. The horizontal velocity data are shown in Fig. 9 for the 12 m depth layer (i.e. 1st bin). Note that despite the vessel being restricted to a minimum depth of 30 m, it was still possible to survey the outer region of this shallow shelf.

The data showed a strong southward flow throughout the survey area, with some attenuation in velocity as would be expected on the shelf with the close proximity of the Agulhas Current. As reported above, measured velocities on the shelf near 9-Mile Reef commonly reach 0.5–0.75 m s^{-1} but rarely exceed this maximum (M. Roberts, unpubl. data). The highest surface velocity in this survey was 120 cm s^{-1} observed offshore in the northern 9-Mile transect and in the south just north of Leadsman Canyon (120 cm s^{-1}). The offshore maxima between these transects were 80 and 100 cm s^{-1}. The mean surface velocity offshore of the shelf edge was *c.* 80 cm s^{-1}. To determine whether these velocity values are common when the Agulhas Current flows close to the shelf edge will require the use of current meter moorings in future studies.

Vertical velocity sections to a depth of 150 m along these transects normal to the shore indicated that velocity not only decreased quite rapidly with depth for all transects, but also that velocities in the water column were lowest in the north (Fig. 10). The horizontal velocity gradient along these transects was more complex than anticipated; a steady offshore gradient of increased velocity at any given depth was expected, and not the zones of lower velocity such as seen in the southern Diepgat Canyon transect.

The satellite SST image shown in Fig. 9 offers an explanation for these unexpected observations: the Agulhas Current proper joins the Maputaland shelf only in the vicinity of Sodwana Bay and appears to have an undulating inshore boundary particularly along the shelf edge. This undulating boundary accounts for both the weaker current velocities measured inside of the 120 cm s^{-1} velocity maximum at 9-Mile Reef and for the complex vertical velocity structure observed along the slope, which ranged between 20 and 80 cm s^{-1} in the depth zone of 100–140 m.

It was not possible to measure velocities accurately using a shipborne ADCP in the canyons due to their narrowness. Nonetheless, very slow and sometimes no currents were detected on *Jago* dives in those canyons where coelacanths were recorded. Also, Trimix divers in Jesser and Wright canyons reported the relative absence of currents just above the substratum. Of course, these anecdotal reports need to be confirmed by a series of velocity measurements using current meters deployed in the coelacanth habitat both inside canyons and on the exposed shelves between canyons.

By comparison, velocities measured in the coelacanth habitat by Hissman *et al.*[4] on the steep slopes of the Comoros Islands were much less than those found off Sodwana Bay, that is, 4.9 cm s^{-1} at 159 m, 3.6 cm s^{-1} at 255 m and 3.1 cm s^{-1} at 273 m. Under these conditions, *Jago* observed coelacanths to move away from their caves at night and to swim slowly along the slopes for distances of up to 10 km. The low-velocity environment no doubt ensured the return of these animals to their caves

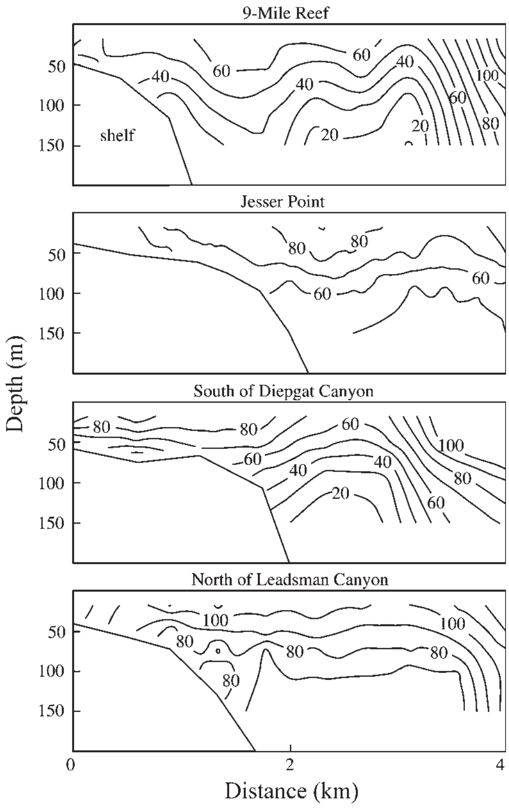

Fig. 10. Vertical velocity sections along shore-normal transects shown in Fig. 9. Contour intervals are 10 cm s^{-1}.

with ease.[4] The low current velocity in canyons, and immediately above the substratum between canyons, enabled coelacanths to migrate within individual canyons and between Wright and Jesser canyons.[2]

One individual (No. 14) moved from Jesser to Wright Canyon, a distance of 4 km, and was then observed again in Jesser three days later,[2] clearly exhibiting mobility along the shelf slope.

Presumably, to move northeastwards (upstream) they would either have to wait for periods of weak current, or use the boundary layer of lower velocity which exists at the water–slope interface.

To understand which of these is applicable requires detailed experiments using deployed current meters and electronic tag telemetry.

Conclusions

1. The seventeen CTD sections collected during four cruises in 2002 and 2003 indicate the temperature range in the Sodwana Bay coelacanth habitat between the depths of 100 and 140 m to be similar to that found in the Comoros Islands, i.e. 15–22°C cf. 15–19°C in the Comoros. This is because these isotherms relative to the Comoros become shallower southwards along the African coast. Because caves and overhangs are also more abundant in the 100–140-m depth range near Sodwana Bay, it is not possible to determine yet which of these two parameters is the most important in determining coelacanth habitat.
2. A 2.5-month-long time series of hourly data collected by a thermistor array deployed near a known coelacanth cave in Wright Canyon indicates this environment to be much more variable than implied by the CTD data, with temperature changes of 16–24°C occurring in a day. This variability is largely caused by the diurnal tide and is greatest during spring tides.
3. The finding of a coelacanth on the shelf edge at a depth of 54 m was coincident with one of the most significant upwelling events between 1994 and 2005, when temperatures at this depth decreased to 17–19°C.
4. Dissolved oxygen levels in this depth zone were found to range between 3.0 ml l^{-1} and 4.8 ml l^{-1} compared to 3.5 ml l^{-1} in the Comoros. The low oxygen values near Sodwana Bay are a result of the SOM, which becomes shallower, as do the temperature isotherms in the southwest Indian Ocean compared to the tropical latitudes and particularly in the Agulhas Current.
5. Current velocities measured using a ship-board ADCP in the depth range 100–140 m at Sodwana were considerably higher than those measured in the Comoros habitat using a current meter (20–60 cm s^{-1} cf. 3–4 cm s^{-1}) and may be an important factor explaining the coelacanth's occupation of the canyons found along the Maputaland shelf-break. However, coelacanths can swim from Jesser to Wright canyon, suggesting that those at Sodwana are not always restricted to the shelter of the canyons by the powerful Agulhas Current.

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